SOUTHEASTERN UNITED STATES AS A CENTER OF GEOGRAPHICAL DISTRIBUTION OF FLORA AND FAUNA.

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CONTENTS.

INTRODUCTION.

From a faunal standpoint, southeastern United States, exclusive of Florida, is very remarkable. The fauna is not only very rich in individuals and species, but also in endemic forms. Some of these are indigenous, while others are evidently fragments of an ancient and formerly widespread fauna. Another fact which increases our interest is the general relationship of this fauna to that of the Northeastern United States, both biologically and geographically, since there can be but little doubt that this area, together with the boreal region, contains the most important centers of distribution for Eastern United States since the Glacial Period. Some of these characteristics are likely to escape notice unless we consider the fauna in its entirety, and not as restricted by geographical limits.

Many of the characteristics of this fauna have long been recognized. It has been well established that the temperate fauna and flora of Northern United States were driven *south* before the ice of the Glacial Period, and that with the retreat of the ice to the

north, a northward migration of life took place. I have hoped that the Postglacial centers of dispersal could be more definitely located than simply in the South, and I have found from a study of geographical relationship of the fauna and flora that one important center has been in *Southeastern* United States, with Chattanooga as the approximate center.

Geographical Affinities of the Temperate Fauna and Flora of Eastern United States.

Several years ago my attention was first attracted toward the Southeast in attempting to get some idea as to the probable geographic origin of our Illinois reptilian and amphibian fauna. I was then led to conclude that this fauna was primarily of *southeastern origin*. At the same time I learned that the flora of the upper Mississippi valley came from the Southeast. MacMillan ('92, p. 653) said of the Minnesota valley, with respect to its higher seed plants: "While continentally central, it is by no means botanically central, but is peculiarly an Atlantic coast and southern region." With regard to the species he says (ibid., p. 717): "As a whole the metaspermatic flora of the Minnesota valley presents itself as distinctly eastern and southern by species as before by genera."[1] Dr. Bessey ('92 and '00) has shown that the trees and shrubs of Nebraska came from the Southeast. He says: "A close study of the foregoing facts as to the distribution of our woody plants shows that nearly all have probably migrated to the plains from the east. . . . Nearly all our trees have come up the Missouri bottoms and spread from the southeastern corner of the state west and northwest." The trees of Kansas clearly show the same origin, as is easily seen by comparing Mason's ('92) list of Kansas trees with the one given by Dr. Bessey.

Cope ('96, p. 895) has pointed out the Eastern origin, or center of distribution, of our fish, amphibian, and turtle fauna. Upon closer analysis this fauna will undoubtedly indicate a *southeastern origin*. I have not been able to learn that students of birds and mammals have especially noticed that Southeastern

[1] By reference to a good contour map of the Mississippi valley, it will be easy to see the highway by which this flora reached this region from the Southeast.

United States is a center of dispersal, yet one can hardly doubt that such will prove to be the case, upon investigation. The annual paths of bird migrations favor this idea. One more illustration will be taken from the fauna. Mr. Bryant Walker's ('98, p. 10) study of the Unionid fauna of Michigan clearly shows that this fauna is almost entirely of Mississippi River origin, and the Mississippi River Unionid fauna is well known to be of *southeastern origin*. But it is not necessary to multiply instances, because the same law holds for the bulk of our fauna and flora and will be recognized by one familiar with any fairly large group of animals. The affinities of both fauna and flora thus point to, and converge toward the Southeast. About the only marked *exceptions* to the rule are the distinctly *northern* or *boreal* groups.

Such illustrations as the foregoing are significant and sufficient to show that to the Southeast is a region deserving of special attention from a faunal standpoint. Because it is believed that here is the natural starting point for an attempt to untangle many faunal and floral problems, evidence has been collected which seems to throw light upon some of its peculiarities.

Richness, or Abundance and Diversity of Life.

As an illustration of the abundance of life, I will consider the flora, which shows a luxuriant development. Sargent ('84, p. 4) says: "Upon the slopes of the southern Allegheny Mountains, and in the valley of the lower Red River, regions of copious rainfall and rich soil, the deciduous forest of the continent attains unsurpassed variety and richness."

The richness of the fauna is shown by both the abundance and size of the individuals. Binney ('85, p. 34) has called attention to this in the case of the land shells of the "Cumberland Subregion" of the southern Appalachians. He says: "If to the 39 species catalogued above as peculiar to this subregion, are added the 69 which inhabit it as a portion of the interior region, it is seen that in the Cumberland subregion we find the largest number of species of any portion of North America. The subregion is equally prolific in individuals, and the individuals are highly developed."

The fresh water molluscan fauna is even richer than the land

shell fauna. Mr. Charles T. Simpson, of the U. S. National Museum, has told me that within 200 or 300 miles of Chattanooga there are more valid species of Unionidæ than in all the rest of the world. As to the Pleuroceridæ, about 300 or 400 species are found in this same area. These and the Viviparidæ here reach their largest size. Here also is the maximum differentiation of the crayfish. The states of Georgia, Alabama and Tennessee, have, according to Faxon ('85, p. 179), the richest crayfish fauna—36 species.

The vertebrate fauna is also very rich. Jordan ('96, p. 114) says of the fish fauna: "These conditions [favorable for fish] are all well realized in the Washita River of Arkansas, in the various tributaries of the Tennessee, Cumberland, and Ohio, and in these streams, among the American streams, the greatest number of species have been recorded."

Endemism and Relicts in the Fauna.

There is still another line of evidence which indicates that this region is not only a recent center of dispersal, but in addition, an area of preservation of ancient types. While it is in this region that the indigenous fauna of Eastern United States reaches its greatest development, it is not these forms primarily to which I wish to call attention now, but to the *relicts* or fragments of a still more ancient fauna. For convenience these will be discussed in two groups:

1. *Relicts having Asiatic Affinities.*—Years ago Asa Gray ('78), and Hooker ('79), and more recently Sargent ('94), have discussed the close relationship existing between many plants found in Eastern America and others found in Japan or Eastern Asia. This discontinuous distribution of many of these forms indicates that they are fragments of an ancient flora. Hooker says: "This generic identity, however, gives but a faint idea of the close relationship between East American and East Asiatic, especially of the Japanese floras, for there is further specific identity in about 230 cases, and very close representation in upwards of 350; and what is most curious is that there are not a few very singular genera of which only two species are known, one from east Asia, the other in east America." The tulip tree (*Liriodendron*), bald

cypress (*Taxodium*), sweet gum (*Liquidambar*), and tupelo or sour gum (*Nyssa*) are interesting examples of genera limited to Eastern Asia and Eastern North America.

But little attention has been given to the Asiatic relationship of the fauna of Eastern United States. No case has come to my notice of a mammal or bird which is limited to *southeastern* United States and shows close East Asiatic affinities. The rodent genus *Zapus* is solely American excepting a single species in Western China (Miller, '00, p. 112). The isolated East Asiatic relative (*Sialia cœlicolor* Hods.) of our common blue bird (*Sialia sialis* L.) is interesting in this connection (Seebohm, '81, p. 328). But our alligator has a near relative in China. The salamander fauna (Gadow, '01, p. 95) of Eastern North America is the richest in the world. *Triton*, as in the case of the dragon-fly *Boyeria*, mentioned below, occurs in Eastern United States, Europe and Eastern Asia. The genus *Amblystoma* is abundant in Eastern North America and has only a single species in Eastern Asia. But the most interesting case among the salamanders is that of the hellbender (*Cryptobranchus alleghoniensis*) whose only near relative is the giant salamandar (*C. japonicus*) of Japan, which attains a length of over five feet. Among fish, Cope ('75, p. 64) gives three genera, the spoon-bill (*Polyodon*), the carpsucker (*Carpiodes*) and a catfish (*Ameiurus*), each represented in China with one species; and Jordan ('96, p. 100) gives the shovel-nosed sturgeon (*Scaphirhynchus*) with relatives in Central Asia.

Among crustacea, the occurrence of *Limulus* upon the Atlantic coast with relatives in Asiatic waters and the freshwater *Peneus* in Eastern United States and also at the foot of the Himalayas (Semper, '81, p. 437), are to the point. Huxley, in his "Crayfish" (p. 334), has pointed out a similar relation among crayfish. Faxon ('85, p. 176) says, concerning this relationship: "The Cambari of Eastern United States are mostly related, not to the crayfishes on the other side of the Rocky Mountains, nor to those on the opposite shore of the Atlantic, but to those of the remotest district, Eastern Asia."

Among insects we have some interesting relicts. For example, we have a dragon-fly (*Hagenius brevistylus*) with its nearest

relative in Japan, and also *Boyeria*, with three species, one species each in Japan, United States and Europe. Our luna moth (*Tropæa luna*) has a close relative in China (*selene* Leach). The Bryozoan genus *Pectinatella*, although mainly of Northern distribution in the United States, has two species, one in Eastern United States, and the other (*P. gelatinosa*) in Japan.

This oriental relationship has been clearly pointed out with regard to some of our Unionidæ by Simpson ('96, p. 330). He says: "The Naiad fauna of this region [Oriental] is magnificent and diversified, and almost rivals that of the Mississippi Valley in vigor, size, solidity and variety of forms. Both Dr. C. A. White and von Ihering believe that the Unios and Anodontas of this area are closely related to those of the central part of North America. Not only does there seem to be a general relationship among a large number of the Naiads of this province with those of the Mississippi basin, but several oriental groups are apparently so close to those of our own region that it is well-nigh impossible to separate them. Thus, the Asiatic Anodontas, typified by *A. woodiana* Lea if found in the United States, would be placed by most students with *A. plana;* the Chinese Unios of the group of *U. housei* Lea, and *myersianus* Lea, are evidently quite near the *Alatus* assemblage; *Unio superbus* Lea, is very much like our *U. capax* Green, and a number of the tuberculate forms of China could almost be placed in the American groups of *U. lachrymosus* and *U. pustulosus*." As has been said before, it is well known that the Unionidæ fauna of the Mississippi River system has been derived from that of Southeastern United States. It is important to notice that the East Asiatic affinities are so distinctly marked in the case of the *fresh water fauna.*

The same explanation which Asa Gray gave for the flora, doubtless holds for the fauna. In Preglacial times the flora had an extensive boreal distribution, as shown by Greenland fossils; and with the advance of the ice, life was driven South in both hemispheres, and has been preserved in both, in favorable localities. An analogous case in the other hemisphere is the preservation of certain mammals in Africa and in the Oriental region (Osborn, '00, p. 57) and Unionidæ (Simpson, '96, p. 340).

Relicts not Showing Asiatic Affinities.

Among animals, there are not only members of this fauna showing close Asiatic affinities, but there are other relicts which do not show such a relationship. Jordan ('88, p. 168) has given a number of genera of lowland fish which he considers archaic forms, or members of an ancient fauna. The mud minnow (*Umbra*), the pirate perch (*Aphredoderus*), the pygmy sunfishes (*Elassoma*), and the blind fishes (Amblyopsidæ), are examples of such forms.[1] Among butterflies *Libythea* is of this type also, and *Tachopteryx* among dragon-flies, and doubtless many other insects are.

Two Centers of Dispersal in Southern United States.

That the South was a retreat for life during the Ice Age is too well known to be discussed here. On account of the great amount of endemism and relicts in the Southeast it seems fair to conclude that quite an abundant and diversified fauna and flora lived there during the Ice Age, although the contrary opinion is often expressed. In south temperate North America there seem to be two very distinct and powerful centers of dispersal, or centers of "adaptive radiation," as Osborn ('00, p. 49) might call them. One, to which we have been calling attention, is in the Southeast, and the other in the Southwest on the arid plateau of Mexico and Southwestern United States. This latter area, or distinct center of dispersal, has a very large number of indigenous forms, as is shown by Merriam's system of zoögeographical areas ('93, p. 401). This is undoubtedly the area where the characteristic arid fauna (and flora)[1] of North America has originated or has had its center of dispersal. The great amount of endemism in this area has suggested that this may have retained much of its present arid condition for a considerable period of time, possibly preceding and during the Ice Age; and one condition of its present richness may be due to its greater distance from the ice-sheet which destroyed many forms in Southeastern United States. The heavy rainfall and forests of Southeastern United States should be contrasted with the arid plains and deserts of the Southwest and the corresponding difference in the types of animals originating in these two regions, noted.

[1] Gray, '81, p. 62, and Bray, '00, p. 713.

Northeastern United States during the Ice Age evidently could have had only a boreal fauna and flora. The present distribution of the boreal fauna and flora is along the northern border of the United States and the higher parts of the Appalachian Mountains. But it is not this element with which we are primarily concerned, because we have seen that the biogeographical affinities of the forms which at present dominate in the Northern United States east of the Great Plains do not point to a boreal origin, nor to the arid region of the plains, nor to the Southwest, but to the *Southeast.*

The criteria, which have been used to determine this center of dispersal will next be considered.

Criteria for the Determination of Centers of Dispersal.

In attempting to determine centers of dispersal of animals, I have found it necessary to keep clearly in mind the tests which are legitimate for such determinations. In a very large number of cases we do not have paleontological evidence in sufficient abundance to materially aid us. For this reason I have thought it desirable to state the criteria used.

1. Location of greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms (Allen).
4. Location of maximum size of individuals (Ridgway-Allen).
5. Location of greatest productiveness and its relative stability, in crops (Hyde).
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence upon a restricted habitat.
8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.
9. Direction indicated by biogeographical affinities.
10. Direction indicated by the annual migration routes, in birds (Palmén).

Some of these tests have long been utilized, but, so far as I have been able to learn, all have not been definitely used for this particular purpose. The fifth (productiveness) is very closely related to the second (dominance). It is very well known that

often plants and animals taken from their indigenous country to a new one, require a very favorable habitat in order to live. Hollick ('93, p. 196) and Cowles ('01, p. 105) have called attention to certain plants of more general distribution in the South, which in the North occur only under very favorable or restricted conditions. This change of habit and habitat with divergence from the center of dispersal is a subject worthy of special attention. If Osborn's law of adaptive radiation is of general application, we should expect just such a change in habitat as has been noticed to accompany the divergence from the original home.

The eighth deserves some special attention on account of the present active interest taken in the study of individual variation, to which reference will be made later. The direction of biogeographical affinities and convergence of lines of dispersal, as has been shown, first called my attention to the Southeast.

Outlets or Highways of Dispersal from the Southeast.

Next in importance to the centers of origin themselves are the highways from and to these regions. From the Southeast we have several very well-marked outlets, as follows:

1. The Mississippi Valley, and valleys of tributary streams: the leading outlet.

2. The Coastal plain, leading along the Atlantic seaboard northward, and along the gulf coast to Florida, and the Southwest.

3. The southern Appalachians and adjacent plateaus, forming an outlet to the North.

These are the principal paths of dispersal; two are lowland, one is upland. The lowland highways have functioned not only for the Southeast, but also for the fauna of tropical origin, as Webster ('98, p. 72) has shown to be the case for the chinch-bug, which has pushed into the United States via Florida and the West Indies and also from Mexico. Of course, these outlets may serve also as inlets from other regions.

Aquatic life has been greatly favored by the Mississippi River system. From the Southeast, the Tennessee River has undoubtedly been the leading outlet; and next, perhaps, the Cumberland River. Formerly the ancient Appalachian River (*i. e.*, the Tennessee above Chattanooga plus the Coosa-Alabama River)

in the Appalachian Valley, was an important highway for aquatic life, and the valley remains to the present time a highway for land forms.

Desirability of Studying the Variations or Modifications in Animals and Plants as They Diverge From Their Center of Origin Along Their Lines of Dispersal.

With the increased interest which is now being shown in the study of individual variations of plants and animals, it is of value to see the relation which such studies have to the highways of dispersal, and vice versa. The real importance of this relation does not seem to be fully realized. This fact is apparent when the geographical variations are largely expressed in terms of the cardinal points, instead of in their relation or deviation from the center of dispersal or changed environment. On account of the topographical relations and past climatic changes of our country, most of the migrations have been deflected more or less to the North or South, and thus such expressions apply in general.

A few points will be mentioned to which special attention is directed:

1. Variation in size, its diminution from the central area. Allen ('76, p. 310) has shown that in North America birds and mammals of austral origin tend to increase in size to the South, while those of boreal origin tend to decrease in size. How general the application of this law is among other animals, has yet to be determined, nor is it known how much the paths of dispersal may influence this. This seems to show concentric divergence from the center of origin. Allen ('71, p. 92) has also called attention to important variations in the size of "peripheral organs" in birds, such as the tail, beak and claws. Weed ('92 and '93) has published two interesting papers on the geographical variations of the harvest-spiders, which show that they increase in size of body and length of legs to the South.

Jordan ('93, p. 23), in speaking of the increase in the number of vertebræ in fish toward the North, says: "In most cases, as the number of vertebræ increases, the body becomes proportionally elongate. As a result of this, the fishes of the Arctic waters are, for the most part, long and slender, and not a few of

them approach the form of eels. In the tropics, however, while elongate fishes are common enough, most of them (always excepting the eels) have the normal number of vertebræ, the greater length being due to the elongation of their individual vertebræ, and not to their increase in number." The relation of these changes to paths of dispersal appears to be close, in some cases at least, as Jordan ('01, p. 566) emphasizes that there is a North and South trend of the lines of distribution of shore fishes.

2. Very closely related to the above law of size and that of dominance of a type in its native home is another formulated by Hyde ('96, p. 575) of the U. S. Department of Agriculture, concerning the productiveness of crops. He says: "Entirely independently of whether the average yield per acre be high or low, the nearer the approach to the region to which a product is indigenous, the more uniform will be the rate of production from year to year; and the farther the departure from such region the greater the liability to fluctuation. This law clearly indicates the greater stability in the indigenous area, and increased variability, with departure from that center. The close relation of the law of size and Hyde's law of productiveness indicates a general tendency which is surely of considerable economic as well as scientific importance, especially with regard to the introduction and acclimatization of foreign plants and animals.

3. The continuity and directness of the individual variations along diverging lines of dispersal is of considerable importance. This fact was impressed upon me by the study of a very extensive collection of gasteropod shells from many localities in the Tennessee River system.[1] There are two very distinct types of shells, which intergrade more or less, in a progressive way, as one passes down stream from the head-waters; one extreme type being in the head-waters and the other farther down stream. It is the degree of continuity or progressiveness in the deviation of the characters which clearly points in definite directions, and emphasizes the necessity of a study of series taken along the lines of dispersal.

In the case of the land fauna the situation is much more complex, yet if highways of dispersal are considered analogous to

[1] Proc. A. A. A. S., 1900.

streams, we are furnished with a good working hypothesis, since the convergence of these lines points to a center of dispersal.

4. The study of variation is essentially a study in biological dynamics, because the lack of stability is the very characteristic considered. The close relation between centers of origin and highways of dispersal emphasizes the desirability of considering faunal and floral areas from the same dynamic standpoint. By this method we can understand the relationships and form of these areas much better. Such areas are *dynamic centers* from which tension lines and zones radiate; and the genetic relationships of these areas can only be determined by a study of the present and past dynamic relations. An important step was made in this direction when Gray and Merriam (Merriam, '90, p. 24) recognized that our North American flora and fauna are composed of *two elements*, boreal and austral, each tending to move from its center of origin.

From a dynamic and genetic standpoint, the limits and significance of life areas take on a new meaning and importance when, as it were, we stand at the center or focus of dispersal, and look outward. From this point of view we look upon the life of a region as constantly diverging or radiating from its original home and the parental stock, encountering new conditions of environment and becoming modified in both habits and structure. The continuity in variations, which is one of the most marked characteristics in the geographical variations, can be safely determined only by the study of the form along its highways. The paths of dispersal are the lines along which we may expect the hereditary factors to show their influence most distinctly. Again, these paths bear the same relation to each other as the branches of a phylogenetic tree, and may therefore be compared with such branches. In phylogenetic studies the most fruitful results do not come from a comparison of the tips of the different branches but from a study and comparison of forms along the same branch and therefore of common descent.

We may with advantage carry this comparison still further, and consider the genetic relationships which faunal areas bear to each other. The lines of kinship are shown primarily along the lines of dispersal. Here, as before, it is not to the relationships which

exist between the terminal branches on which we are to focus our attention, but to those affinities which exist along the highways toward the center of origin. The double origin of the North American fauna and flora will illustrate the present standpoint. The lines of dispersal may be represented by two trees, one with its roots in the North, and the other with its roots in the South, and whose branches intermingle. From these two centers, life has radiated in all possible directions, but on account of the North and South trend of the topography the lines of dispersal have, in the main, been North and South. For this reason the general lines of kinship are likely to be most strongly expressed in these same directions.

It is a very fundamental law that most forms of life are confined to restricted areas and only a small number have extensive distribution. Thus, from the centers of origin there is a constant decrease, or *attenuation* in the number of forms which have been able to depart far from the original home. From this standpoint, therefore, the question arises as to what criteria are to be used in the determination of life areas. Should more stress be laid upon the concentric relations, or degree of attenuation, from the center of dispersal, or, on the other hand, upon the genetic affinities, such as exist along the lines of dispersal? Are the natural affinities better expressed zonally or dendritically? In one case the tree is horizontally truncated and in the other the branches are torn apart.

Surely the genetic and dynamic standpoint, which attempts to explain the life of an area in terms of its origin, favors, as a working hypothesis, a trial of the dendritic method. The method of work here suggested will put faunal studies upon a *distinctly genetic basis.*

From the relationship which exists along the lines of dispersal, we draw an important practical conclusion. In collecting a series of animals for the study of variation, one of the first things to be done is to determine its means and highways of dispersal and then secure material from along these lines. This will greatly simplify the study of land forms, because in this manner we have a clue to determine which localities are likely to be the most important, and upon these we may concentrate our attention.

5. The geographical distribution of color variations is a subject which it is very desirable to study from the standpoint of geographic origin as well as from that of climatic influences. Allen ('71, '72, '74, '77 and '92), especially, has given much attention to the formulation of the laws of geographic color variation among North American birds and mammals, and correlates some of these variations with that of moisture. Ridgway ('72) has also an important paper on color variations in birds. Keeler ('93) and Hasbrouk ('93) are referred to for further information on color variations. These papers give numerous cases showing that species of wide distribution change in color in different localities. These papers cannot be discussed here, but deserve to be much better known.

Summary.

First. In general the fauna and flora of Northern United States East of the Great Plains are geographically related to those of the Southeast and this geographical relationship points to an origin in the direction of the Southeast except in the case of the distinctly boreal forms.

Second. The abundance and diversity of life in the Southeast indicates that it has been, and now is, a center of dispersal.

Third. The relicts indicate that the Southeast has been a center of preservation of ancient types, and the endemism shows that it has been a center of origin of types.

Fourth. There are two distinct Southern centers of dispersal in temperate United States; one in the moist Southeast, and the other in the arid Southwest.

Fifth. Ten criteria, aside from fossil evidence, are recognized for determining the center of origin or the locality of dispersal:

1. Location of the greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms. (Allen.)
4. Location of maximum size of individuals. (Ridgway, Allen.)
5. Location of greatest productiveness and its stability, in crops. (Hyde.)
6. Continuity and convergence of lines of dispersal.

7. Location of least dependence upon a restricted habitat.

8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.

9. Direction indicated by biogeographical affinities.

10. Direction indicated by annual migration in birds. (Palmén.)

Sixth. There are three primary outlets of dispersal from the Southeast:

1. The Mississippi Valley and its tributaries.

2. The Coastal Plain.

3. The Appalachian Mountains and adjacent plateaus.

The first two have also functioned for tropical types, and the third for boreal forms. Dispersal is both forward and backward along these highways.

Seventh. The individual variations of animals and plants, such as size, productiveness, continuity of variation, color variation, and change of habit and habitats, should be studied along their lines of dispersal and divergence from their center of origin. Life areas should be studied as centers of dispersal and origin, and hence *dynamically* and *genetically*.

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